THE FLORAL BIOLOGY OF PLATANTHERA DILATATA (PURSH) LINDL. (ORCHIDACEAE)

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The Floral Biology of *Platanthera dilatata* (Pursh) Lindl. (Orchidaceae)

by

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Abstract

The floral ecology of Platanthera dilatata (Pursh) Lindl. in St. Phillip's, Newfoundland, was investigated during the 1990-1992 flowering seasons. For comparison, two additional populations from eastern Newfoundland and a population from southwestern Alberta were also examined. Pollinators were restricted to the nocturnal Noctuidae and diurnal Hesperiidae. While pollinators were rarely observed, pollination exclusion experiments indicated that insect vectors are required for capsule set. Percentage capsule set for the St. Phillip's site was similar in all three seasons (range = 47.7-56.0%). Two populations from eastern Newfoundland showed similar capsule set values while the population in southwestern Alberta had significantly higher capsule set (66.8%). Capsule set was determined to be pollinator-limited. Microhabitats had no effect on capsule set. P. dilatata has a number of physical characteristics which increased its opportunity for pollination. These include an extended blooming period, sequentially-produced flowers which are long-lived, long receptivity-time for flowers and continual odour production. The adaptations are particularly advantageous during periods of unfavourable weather and low pollinator activity. Additionally, it was observed that some populations can have seed production dramatically reduced due to insect damage and fungal infection.

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1. Introduction

1.1 The Orchidaceae

The Orchidaceae, the largest and most highly evolved family in the subclass Monocotyledonae (Dressler 1981), is highly specialized, especially with respect to the mode of pollination (Luer 1975), and they show a high degree of specificity in pollinator-plant interactions. Detailed studies on this aspect of the Orchidaceae have only been attempted recently (Dressler 1981).

The floral biology of the Orchidaceae has fascinated botanists for many years. Darwin (1887) recognized that in their natural state orchids are characterized by highly specialized flowers and low levels of fruit set (Darwin 1887). Since Darwin's time, orchidologists have sought to explain the precise pollination mechanisms of orchids. Interest in the pollination ecology of temperate North American orchids has increased substantially in the last 10 years (Catling 1981, Hogan 1982, Cole and Firmage 1984, Patt et al. 1989, Primack and Hall 1990, Robertson and Wyatt 1990, Boland and Scott 1991), however, few studies have followed an orchid population for more than one flowering season (Cole and Firmage 1984, Firmage and Cole 1988, Calvo 1990, Robertson and Wyatt 1990).

The Orchidaceae is the only family of monocotyledons known for the consolidation of pollen grains into discrete masses referred to as pollinia. These pollinia are attached to small stalks, the caudicles, which are united to a sticky disk of cells, the viscidium. Together, these structures form the pollinaria. When a pollinator visits an orchid flower, the entire pollinaria may be removed and later deposited, in its entirety or its parts, onto the stigmatic surface of another recipient flower. Such a strategy has been referred to by Van der Pijl and Dodson (1966) as "precision gambling"; basically, a one-shot system capable of fertilizing a large number of ovules. Orchid capsules may contain as few as 1330 seeds in Coeloglossum viride (L.) Hartm. or more than 4 million in Cycnoches ventricosum Batem. (Arditti 1966). This strategy can lead to high reproductive output even when the plant is exposed to low pollinator activity.

Most studies on the floral biology of orchids have attempted to determine pollinator activity by direct observation of the pollinator's visits and by calculating mean capsule set (Smith and Snow 1976, Ackerman and Mesler 1979, Cole and Firmage 1984, Catling and Catling 1989, Vogt 1990). Determination of which flowers have been visited or pollinated is simplified in orchids due to their production of pollinaria. Inspection of an orchid flower can determine if the pollinaria have been removed or if any pollinia have been

deposited on the stigmatic surface. Surprisingly few studies have taken advantage of this aspect of pollination in orchids to acquire further knowledge about levels of pollination in orchids (Ackerman 1975, Firmage and Cole 1988, Robertson and Wyatt 1990).

1.2 Purpose

The purpose of this study was to investigate the floral ecology of the scent-bottle orchid, Platanthera dilatata (Pursh) Lindl. P. dilatata is often referred to as "bog candles" or tall leafy white orchis. Locally, many Newfoundlanders refer to them as "scent-bottles". To date, no thorough scientific study has been done on this orchid. Other orchid researchers make brief mention of the pollinators of this orchid, but only say it is pollinated by various noctuid moths (Catling 1985) and skippers (Luer 1974). No other details of the reproductive biology are known.

Many factors may affect the reproductive success of P. dilatata. These include resource availability, weather conditions, pollinator abundance and plant predation (Wyatt 1982). Microhabitats, too, may have an affect on the reproductive rates of an orchid (Smith and Snow 1976, Cole and Firmage 1984). Pollinator attraction may also be influenced by the phenology of the orchid and the size of their

inflorescence.

The specific objectives of this study were: 1) to determine what levels of fruit set occur within and between years in several natural populations; 2) to identify pollen vectors; 3) to determine the breeding system; 4) to examine reproductive success in relation to inflorescence size, phenology, site location and microhabitats.

To date, most studies on the reproductive biology of non-autogamous orchids (i.e., those which do not self-pollinate) have found them to be pollinator limited (Schemske 1980, Cole and Firmage 1984, Berry and Calvo 1991, Gregg 1991). This study examines how the preceding factors affect reproductive success in P. dilatata and whether this orchid, like many others, is pollinator limited.

1.3 The genus Platanthera

1.3.1 Classification

The genus Platanthera is one of the largest genera of orchids in the north temperate zones (Inoue 1983). There is much disagreement about how many species of Platanthera exist. Some authors give a modest estimate of about 80 species

(Davies and Huxley 1988) while others are more generous, at approximately 200 species (Luer 1975). This is just one example of the problems which exist in orchid research.

Originally, all Platanthera species were classified in the genus Orchis (Brackley 1985). Orchis was described by Linnaeus in 1753, and included any terrestrial orchids with fleshy tubers, a leafy stem and a terminal spike of spurred flowers (Luer 1975). In 1805, Willdenow reclassified the present day Platanthera as members of the genus Habenaria. He made his decision based on differences in the column structures. L.C. Richard, in 1818, segregated Habenaria from a group of orchids whose pollinia caudicles were adnate to the column (Brackley 1985) and placed them in the genus Platanthera. However, although established as early as 1818, the genus Platanthera has only recently been widely accepted.

Platanthera differs from Habenaria by its simple median stigma located above the nectary opening while Habenaria has two stigmatic lobes borne on stalks beside or below the nectary opening (Stoutamire 1974). Other differences between Platanthera and Habenaria are based on their sinkers. The term "sinker" is used to describe the root system of these orchids. The sinkers of Platanthera are either fusiform or stoloniferous while those of Habenaria are globose (Inoue 1983). They also differ ecologically; Platanthera is

distributed in temperate regions while Habenaria is mostly tropical to sub-tropical.

The study species is a member of the Platanthera dilatata- Platanthera hyperborea complex, often referred to as the section Limnorchis. This section is characterized by a leafy stem which terminates in an elongate spike of small white to greenish flowers. The anther locules are divergent and the caudicle is nearly one half the length of the pollinarium. The viscidium is suborbicular and the stigma is somewhat flattened and broadly rhombate (Inoue 1985).

Rydberg (1901) created the genus Limnorchis for this species-complex and divided it into 24 species (Luer 1975). However, this nomenclature is not widely accepted, thus for the purpose of this study, the species of interest will be described as a member of Platanthera.

This section has representatives in both North America and Japan. The group has its center of diversity in North America, with Japan at the limit of its range. The chromosome number in North America is 2n=42, while Japanese plants are tetraploid 2n=84 (Love and Ritchie 1966, Love and Love 1980). Some members of the group are autogamous (Inoue 1985).

There are five species of the section Limnorchis in North America. P. dilatata is the only white-flowered species; the others have greenish flowers. The other four species include P. hyperborea (L.) Lindl., P. sparsiflora (S. Wat.) Schlecht., P. limosa Lindl. and P. stricta Lindl. A tentative sixth species (or subspecies), P. huronensis (Nutt.) Lindl., was originally included with P. hyperborea, however, unlike P. hyperborea which is autogamous, the flowers of P. huronensis require an insect vector.

Many plants with wide distributions can have some morphological variations between different areas, especially among allopatric populations. Such is the case with P. dilatata. Luer (1975) recognizes three distinct varieties. P. dilatata var. dilatata is the typical form. It is distinquished by having the lip and spur of equal lengths. The variety leucostachys (Lindl.) Luer is distinquished by its more slender spur which is twice the length of the lip or ovary. The variety albiflora (Cham.) Ledeb. differs from the others in having a short, thick spur, half the length of the lip, and slightly larger flowers on a more compact spike (Luer 1975). These varieties are believed to have arisen in response to different pollinator groups (Luer 1975).

1.3.2 Morphology

Most Platanthera species are terrestrial, although some may be considered semi-aquatic. Morphologically, Platanthera has fleshy, tapered or swollen roots. Early in the growing season, a bud is produced on the "sinker". This bud produces its own roots during the rest of the growing season, however the bud does not develop any further. At the end of the growing season, the old plant deteriorates, leaving only the bud with its own roots. In the subsequent growing season, the bud will develop into a leafy plant (Case 1964).

Plants are erect with basal or cauline leaves. The stem is terminated by a raceme of relatively small flowers. The petals often adhere to the dorsal sepal to form a hood-like structure over the column, while the lateral sepals are spreading or recurved. The lip may be entire, divided or fringed, depending on the species (Luer 1975).

Platanthera flowers have a spur at the base of the lip, and the length of the spur often corresponds to the proboscis-length of a species or specific group, generally of the Lepidoptera (Luer 1975). The opening to the spur is located below the stigma on the column (Case 1964). The column, or gynandrium, is a feature common to all orchids and represents a fusion of three structures; the stamen, the stigma and the

style. Two anthers are borne on either side of the column and are separated from each other by connective tissue or the stigma. The pollen grains are compressed into masses known as pollinia. The pollinia are attached to caudicles which are narrowly united to a sticky disc of cells called the viscidium (Nilsson 1978). The entire structure is club-shaped and is termed a "pollinarium" (Dressler 1981). The two pollinaria are embedded in locules on either side of the nectary opening, with the adhesive discs of the viscidia facing each other. The distance between the viscidia often corresponds to the head width of the specific pollinating insect. As the insect probes the nectar-containing spur with its proboscis, the viscidia adhere to the eyes or proboscis of the pollinator. When the insect leaves the flower, it pulls the pollinaria from its locules (Brackley 1985). Within about a minute, the caudicles rotate downward and inward as one side of each caudicle dries, causing the pollinaria to be located in a forward position. The pollinaria are now in a position to come directly in contact with the stigma of the next visited flower (Smith and Snow 1976, Nilsson 1978, Cole and Firmage 1984).

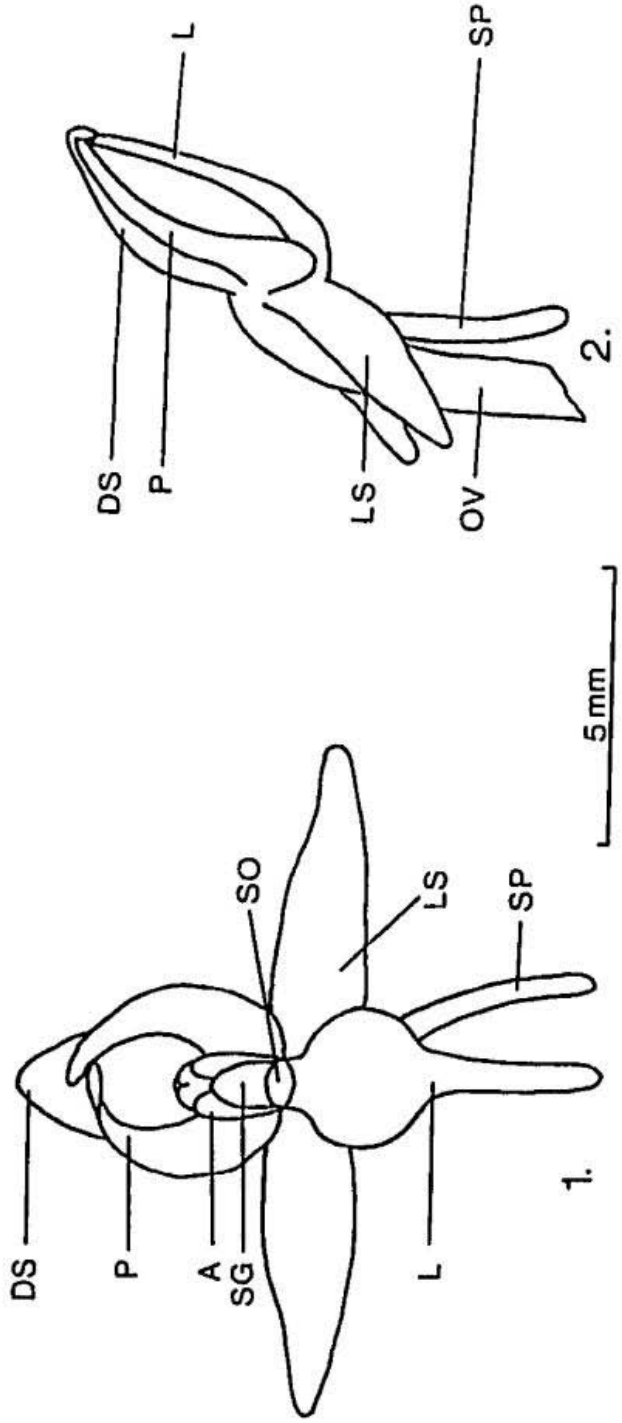
The stem of P. dilatata arises from elongate fleshy roots. The several glabrous leaves are linear-lanceolate, clasping the stem below and becoming bract-like above. The inflorescence is a loose to densely flowered cylindrical

spike. The white flowers are subtended by ascending, lanceolate floral bracts. The dorsal sepal is ovate, obtuse and concave. The lateral petals are elliptic-lanceolate and connivent with the dorsal sepal, forming a hood-like structure. The lip is linear-lanceolate and abruptly dilated (hence the species name, dilatata) at the base (see photograph, Figure 1). The cylindrical spur is approximately the same length as the lip (Case 1964, Luer 1975). The nectary is located near the end of this spur (Figure 2). These features characterize flowers pollinated by moths (Faegri and Van der Pijl 1979). The flowers are strongly clove-scented, both by day and by night, a feature atypical of moth-pollinated plants which normally produce fragrances only at night (Van der Pijl and Dodson 1966). Quite often, the flowers of P. dilatata maintain a half-opened appearance. This occurs when the tip of the lip catches in the hood formed by the dorsal sepal and lateral petals. This phenomenon appears to be more common on the upper flowers of the floral spike.

Members of the genus Platanthera generally fall into one of two pollinator categories; either moth-pollinated or butterfly-pollinated but, as previously noted, there are exceptions. In either case, the orchids possess certain morphological adaptations to the behaviour and morphology of the primary pollinator group (van der Pijl and Dodson 1966).

Figure 1. Close-up photograph of an inflorescence of *P. dilatata*.

Figure 2. Details of the flower characteristics of P. dilatata. 1. Front view of fully opened flower. 2. Lateral view of upper flower showing the lip "caught-up" in the hood. A, anther; DS, dorsal sepal; L, lip; LS, lateral sepal; OV, ovary; P, petal; SG, stigmatic surface; SO, spur opening; SP, spur.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The major isolating factors preventing cross-pollination between different species of Platanthera in a particular region are the blooming date of the species, the insect or group of insect pollinators and where the pollinaria are deposited (Table 1).

1.3.3 Distribution

Platanthera is most abundant in North America and eastern Asia. Europe has only two species of Platanthera (Davies and Huxley 1988) while the relatively small area of Japan has 21 endemic species (Inoue 1983). The North American flora contains 24 species (41 taxa), 11 (14 taxa) of which are found on the island of Newfoundland (Luer 1975). Platanthera species are among the most readily encountered orchids in Newfoundland (personal observation).

P. dilatata has the second widest distribution of any North American terrestrial orchid. The scent-bottle ranges from Greenland and Newfoundland west through boreal North America to the Aleutian Islands. In the east, plants are distributed as far south as New Jersey, northern Indiana and

Table. 1 Overview of the known pollinator groups for the Platanthera of Newfoundland.

species of orchid	pollinator group
Platanthera albida	autogamous (Catling 1983)
P. blephariglottis	butterflies, hawkmoths, skippers, Bombus spp. - pollinia attached to eyes (Cole and Firmage 1984)
P. clavellata	autogamous (Catling 1983)
P. dilatata	noctuid moths, skippers - attachment site undocumented (Luer 1974)
P. grandiflora	hawkmoths, Papilio spp. (?) - pollinia attached to eyes (Stoutamire 1974)
P. hookeri	skippers - pollinia attached to eyes (Luer 1974)
P. hyperborea	autogamous (Catling 1983)
P. lacera	hawkmoths - pollinia attached to proboscis (Stoutamire 1974)
P. obtusata	mosquitoes, geometrid and pyralid moths - pollinia attached to eyes (Thien and Utech 1970, Voss and Riefner 1983)
P. orbiculata	hawkmoths, noctuid moths - pollinia attached to eyes (Stoutamire 1971)
P. psycodes	hawkmoths, skippers, Papilio spp. - pollinia attached to proboscis (Stoutamire 1974,

Illinois. In the west, plants extend farther south in the mountains to southern California, northern New Mexico and Colorado (Luer 1975).

The variety dilatata is found throughout the distributional range noted above. Variety leucostachys is found in high altitude wet meadows and fens of the Pacific Northwest. In Alaska, variety dilatata and variety leucostachys are largely replaced by the variety albiflora. This variety extends south of Alaska, to the northern American Rockies (Luer 1975).

1.3.4 Habitat of P. dilatata

P. dilatata grows in a variety of habitats throughout its wide distributional area. In the east and north, it commonly grows in wet open fens, but is also found along lakeshores, marls, wet sands and damp roadsides (Case 1964). Throughout much of western North America, scent-bottle orchids are most commonly encountered along alpine and sub-alpine streams and small alpine mountain fens (Williams 1980).

This orchid is most abundant in the northern areas of its range, becoming quite rare in its southernmost areas. Generally it is rare throughout its distributional range in the U.S.A. (Luer 1975).

The habitat of P. dilatata on the island of Newfoundland changes from east to west. On the Avalon Peninsula, P. dilatata is mostly restricted to nutrient-rich fens where they often grow in deep sphagnum beds. In contrast, Case (1964) states that in the Great Lakes region, P. dilatata never grows in sphagnum beds. While far from rare on the Avalon, they are generally only locally common. They are much more common in western Newfoundland where they are present in fens, damp meadows, roadsides and seepage slopes of the Long Range Mountains.

1.3.5 Blooming Season

The flowering season of P. dilatata ranges from May in the south, June and July around the Great Lakes, and August in the north (Luer 1975). The blooming season of P. dilatata on the island can be quite variable. The climate of western Newfoundland is more continental than that of the Avalon and plants bloom as early as late June. In contrast, populations on the Great Northern Peninsula and Avalon Peninsula, rarely begin to bloom prior to mid-July and may still be blooming in late September (personal observation).

1.4 Previous Studies on the Pollination of *Platanthera*

In North America, much orchid research has been carried out on *Platanthera* (Stoutamire 1974, Smith and Snow 1976, Cole and Firmage 1984, Sheviak and Bowles 1986, Patt *et al*. 1989, Robertson and Wyatt 1990). The genus is generally considered to be pollinated by members of the Lepidoptera (van der Pijl and Dodson 1976) which includes moths, skippers and butterflies. *P. ciliaris* (L.) Lindl. appears to be pollinated exclusively by butterflies (Smith and Snow 1976) while *P. orbiculata* (Pursh) Lindl. is pollinated by moths (Stoutamire 1971). However, not all members of the genus *Platanthera* have such specialization; *P. obtusata* (Pursh) Lindl. is pollinated by mosquitoes as well as moths (Stoutamire 1968, Voss and Riefner 1983); *P. blephariglottis* (Willd.) Lindl. has both bee and lepidopteran pollinators (Cole and Firmage 1984), while *P. stricta* has fly, bee and lepidopteran pollinators. Thus, while some platantherans are more specific with respect to pollinator groups, others are more generalized. Table 1 summarizes the known pollinator groups for the *Platanthera* of Newfoundland.

2. Materials and Methods

2.1 Site Description

The major portion of this study was conducted at a small fen located 0.7 km south of the Town of St. Phillip's Town Hall (47° 35' 33" N, 52° 51' 24" W). The area of this fen was approximately 0.75 km^2. Field work was undertaken during July, August and September of 1990, 1991 and 1992.

This fen was characterized by three distinct vegetative zones. Along the edge of the fen was a tree and tall shrub zone dominated by black spruce (Picea mariana (Mill.) BSP.), larch (Larix laricina (DuRoi) K. Koch), sweet gale (Myrica gale L.), meadowsweet (Spiraea latifolia (Ait.) Borkh.) and northern wild raisin (Viburnum cassinoides L.).

Adjacent was a low shrub zone which included swamp rose (Rosa nitida Willd.), fly honeysuckle (Lonicera villosa (Michx.) R.& S.), leatherleaf (Chamaedaphne calyculata (L.) Moench), labrador tea (Ledum groenlandicum Oeder) and common juniper (Juniperus communis L.).

The central area of the fen was an open mat zone dominated by sedges (Carex spp.), sphagnum moss (Sphagnum spp.), marshberry (Vaccinium oxycoccus L.), meadowrue

(Thalictrum polygamum Muhl.), bog aster (Aster nemoralis Ait.) and bog goldenrod (Solidago uliginosa Nutt.).

The boundaries between these vegetative zones were not discrete, thus the open mat zone could extend into the low shrub zone and rarely into the tree-tall shrub zone.

The population of flowering P. dilatata ranged from 489 in 1992 to 549 in 1990. This orchid was found in a variety of microhabitats including open areas, among low shrubs and obscured under taller shrubs and trees.

During 1992, two other sites were also studied, but in less detail. One site was located in Butterpot Provincial Park (47° 24′ 15" N, 53° 02′ 15" W). This site was a small fen located on a seepage slope in a barren region. It was dominated by sedges (Carex spp.), cinnamon fern (Osmunda cinnamomea L.), marshberry (Vaccinium oxycoccus) and other dwarf ericaceous shrubs. A total of thirty plants of P. dilatata was studied in this site.

The other site was located at Cape Freels, Bonavista Bay (49° 14′ 03" N, 53° 26′ 50" W). This site, located within 100 m of the open ocean, was a damp open meadow dominated by black sedge (Carex nigra (L.) Reichard), grasses (Poa spp., Festuca spp.), common buttercup (Ranunculus acris L.), white clover

(Trifolium repens L.) and wild strawberry (Fragaria virginiana Duchesne). Thirty plants were studied in this site.

A final site, examined in 1990, was an alpine fen located on the eastern edge of Lake Cameron in Waterton Lakes National Park, Alberta (49° 01' 31" N, 114° 03' 24" W). This site was dominated by dwarf willow (Salix spp.), prickly rose (Rosa acicularis Lindl.), grasses, rush (Juncus spp.) and several species of indian paintbrush (Castilleja spp.). Thirty plants of P. dilatata were studied in this site.

2.2 Data Collection

Flowering orchids from the St. Phillip's site were classified as belonging to one of three microhabitats; 1) plants which were obscured under trees or tall shrubs, 2) plants growing adjacent to trees or shrubs, but exposed, and 3) plants growing on the open mat.

The site was visited every second day and the total number of plants, which were in bloom or faded, was noted. Within each microhabitat, several features of the plants were determined. These included the total number of plants within the microhabitat, the height of the plants from the substrate surface to the tip of the inflorescence, the number of flowers

and seed capsules per inflorescence and the length of the inflorescence.

Morphological measurements were taken randomly from fifteen flowers on separate plants. The following measurements were made: the width and length of the dorsal sepal, lateral sepals, petals, lip and the nectar spur. These measurements were then compared with those previously documented for P. dilatata in Case (1964) and Luer (1975).

The breeding system of P. dilatata was determined through a series of pollination experiments. To test for autogamy (self-pollination), ten inflorescences (232 flowers) were enclosed within fine 1 mm nylon mesh prior to the opening of the first bloom. This prevented any insect visitations.

For more precise pollination experiments fifteen plants were removed from the field and grown in a coldhouse. Eighty-two flowers on four inflorescences were self-pollinated. Ninety-seven flowers on four inflorescences were pollinated geitonogamously; i.e., pollinated with pollinaria from another flower on the same spike. One hundred and fifteen flowers from four inflorescences were cross-pollinated (xenogamy). Pollinaria for cross-pollination were removed from the flowers with a toothpick, then placed on the stigmatic surface. The remaining unpollinated plants were examined to determine the

lifespan and receptivity of individual flowers. As each individual flower opened, it was marked with coloured thread and the date recorded. Once all flowers on a spike were opened, they were cross-pollinated.

Pollinator activity was observed in the field at various times of the day to optimize the probability of observing floral pollinators and visitors. Observation periods varied in length from 1 to 4 hours. Pollinators were determined as those insects with pollinaria attached, while visitors were those which probed the flowers but did not remove pollinaria. These insects, where possible, were captured with a net and identified later. Some insects had an "uncertain" pollinator status since they escaped before they could be caught and examined.

The flowers of P. dilatata open sequentially over an extended period. To gain insight into changing pollinator activity throughout the flowering period, each inflorescence was divided into thirds and the number of seed capsules formed in each third was recorded.

During the 1992 field season, pollinator activity was further examined by recording pollinaria removal and deposition rates and whether this activity occurred mostly at night or by day. Fifteen plants were covered with fine nylon

mesh which was then removed on August 10. At this time, a minimum of 70% of the flowers was open on each spike. These plants were then observed twice daily, at 8:00 am and at dusk (approximately 7:45 pm) for a total of 10 days. These times were chosen to represent the day-time versus night-time periods. During each visit the number of pollinaria removed or deposited on the stigmatic surface was noted.

To determine if density affects pollination rates, nine isolated patches of plants were examined. These patches contained 1 (5 replicates), 5, 10 and 20 plants per square metre, respectively. These patches were no less than 50 m apart, with no plants of P. dilatata in between.

During the 1991 and 1992 field season, plants from the St. Phillip's site were examined to determine the amount of insect damage to the inflorescences. For each inflorescence collected, the number of seed capsules with insect damage was noted, then analyzed to determine if insect damage was associated with the microhabitat of the orchid or with the number of capsules produced per plant. Insect damage was noted in the form of small holes or furrows within the developing capsule as well as the consumption of ovules.

During mid-September of 1992 thirty plants from both the Butterpot and Cape Freels sites were also examined and data

collected on plant height, inflorescence length, number of flowers, number of capsules and insect damage. Thirty plants from the Cameron Lake, Alberta site were examined in the same manner in early September of 1990 for comparison.

2.3 Data Analyses

All data were tested for normality using the procedure outlined in the Minitab Reference Manual (1988). Homogeneity of variance was determined using the F-test statistic.

As recommended by Sokal and Rohlf (1981), arcsin transformation was applied to the capsule set percentages for each treatment. Mean capsule set percentages within treatments were calculated in transformed scale and then retransformed (Rohlf and Sokal 1969).

Transformed means were compared using the Tukey-Kramer method of multiple pairwise comparison for unequal sample sizes and the T-Method of multiple pairwise comparisons for equal sample sizes (Sokal and Rohlf 1981). All other calculated means used these two methods or ANOVA. Statistical significance for all statistical methods is taken to be at the 5% level.

Insect damage was not normally distributed, thus, to

determine if insect damage was associated with the number of seed capsules produced per plant, the two variables were compared using the Spearman's Rank Correlation Coefficient (McClave and Benson 1982).

3. Results

3.1 Results of Within-site Study at St. Phillip's

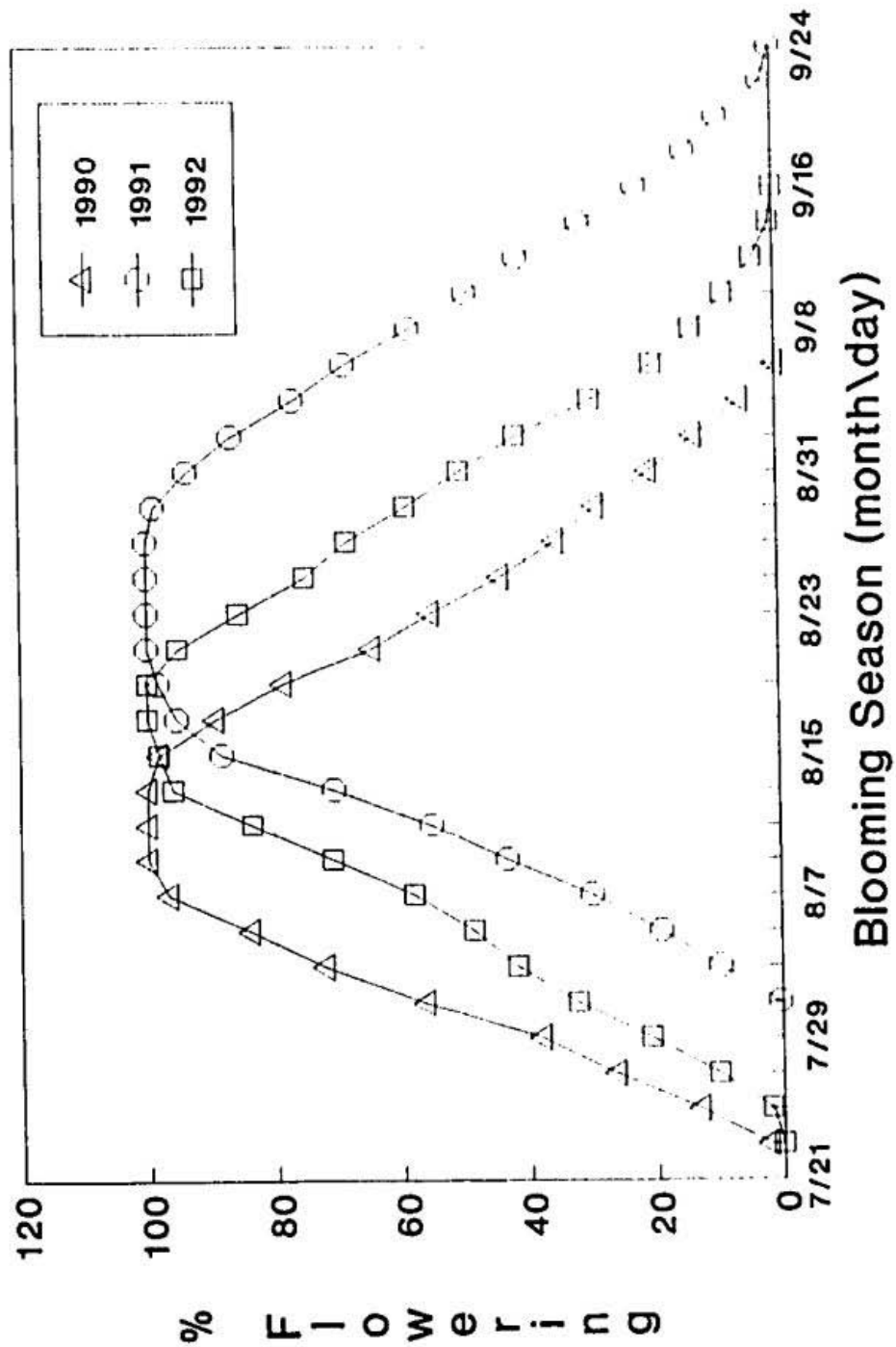
3.1.1 Phenology

Anthesis occurred at the St. Phillip's site on July 23, 1990; August 1, 1991; and July 25, 1992. The percentage of plants (n_{1990}= 549, n_{1991}= 538, n_{1992}= 489) in bloom over their entire flowering season is presented as a combined phenology curve (Figure 3).

The times of peak bloom for P. dilatata differed by as much as 14 days during the three summers. The earliest peak was on August 7, 1990, the latest on August 21, 1991. The flowering season averaged 51 days (range = 43-59 days). Plants required an average of 12.4 days (range = 3-24 days, n = 152) for all flowers on an inflorescence to open. The average lifespan of an individual flower was 17.2 days (range = 12-22 days, n = 184). Flowers remained receptive to pollinia up to the day of senescence. Pollinated flowers acquired brown stigmas, but otherwise did not undergo any postpollination changes until they senesced. In contrast, most orchid flowers quickly senesce once a pollinium is deposited on the stigmatic surface.

The major nectar sources available at this site concurrently with P. dilatata were Aster nemoralis, Solidago

Figure 3. Percentage of total P. dilatata inflorescences open (1990-1992).


1990
1991
1992
% Flowering
120
100
80
60
40
20
0
7/21
7/29
8/7
8/15
8/23
8/31
9/8
9/16
9/24
Blooming Season (month\day)

uliginosa, Rosa nitida and Thalictrum polygamum. Rosa and Thalictrum were mostly faded prior to the peak blooming of P. dilatata so they would not compete for the attentions of potential pollinators. The blooming seasons of Solidago and Aster overlapped with that of the orchid. Observations of pollinators showed Bombus spp., syrphid flies, butterflies and skippers to visit these co-blooming plants.

3.1.2 Flower Production and Morphological Comparisons

The number of flowers per inflorescence varied from 6 to 62 but, for the three summers of study, the mean number of flowers produced per plant was similar (range = 27.6-30.6; Table 2). The distribution of the number of flowers was normally distributed during the three seasons (Figure 2). The mean inflorescence length and mean plant height were comparable among the three summers (Table 2).

P. dilatata grew in a number of different microhabitats; most commonly on the open mat and least commonly obscured under trees and shrubs (Table 3). The mean number of flowers per inflorescence did not differ significantly among the three microhabitats studied (Table 4). However, the mean plant heights and mean inflorescence length did show significant microhabitat differences (Tukey-Kramer method; Table 5, 6).

Table 2. Summary of means (±95% C.I.) obtained over the seasons of 1990-1992 from a population of P. dilatata growing in St. Phillip's.

Year	mean # flowers per plant	average % capsule set per plant	mean inflorescence length per plant (cm)	mean plant height (cm)
1990 n=74	27.6 (1.9)	47.7 (5.7)	8.4 (0.5)	38.1 (1.8)
1991 n=113	30.6 (2.3)	56.0 (3.6)	8.7 (0.5)	37.6 (1.3)
1992 n=94	27.7 (1.8)	52.4 (4.1)	8.6 (0.4)	37.2 (1.3)
Total	28.6 (1.0)	52.0 (2.3)	8.5 (0.3)	37.6 (0.8)

Figure 4. Frequency distribution of flowers per individual (1990-1992).

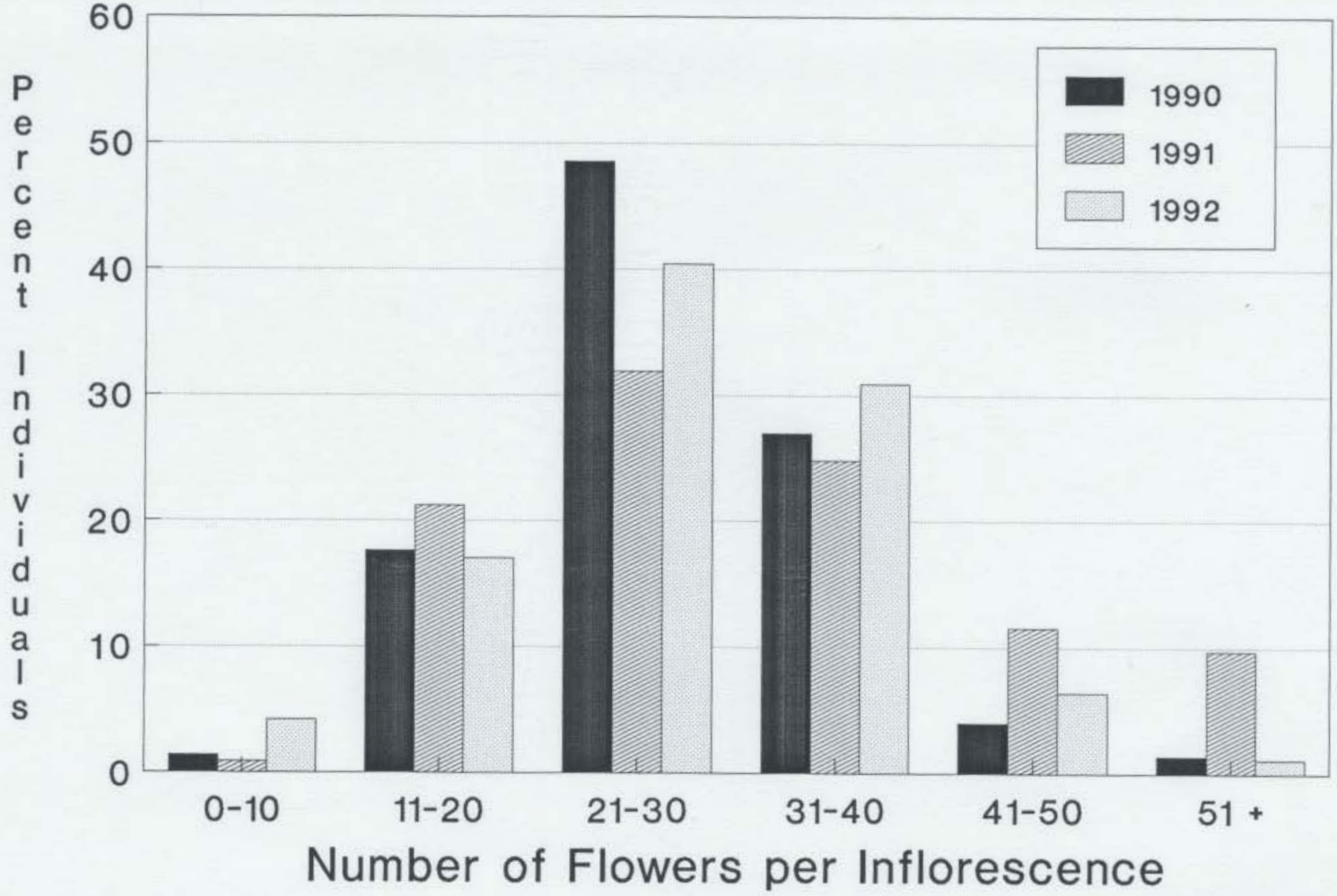

60
50
40
30
20
10
0
Percent Individuals
1990
1991
1992
0-10
11-20
21-30
31-40
41-50
51 +
Number of Flowers per Inflorescence

Table 3. Total number of flowering plants found in each of the microhabitats within the St. Phillip's study site.

year	open mat	shrub zone	obscured areas	total
1990	424	95	30	549
1991	417	91	30	538
1992	382	78	29	489

Table 4. Average number of flowers per inflorescence (±95% C.I.) of P. dilatata in relation to microhabitats at the St. Phillip's study site.

year	open mat	shrub zone	obscured areas
1990	25.2 (3.0) n=21	27.4 (3.0) n=36	31.2 (4.8) n=17
1991	30.5 (4.1) n=42	30.8 (3.6) n=47	30.5 (4.8) n=24
1992	27.1 (3.6) n=31	27.6 (3.0) n=41	28.5 (3.4) n=22
Total	27.6 (2.0)	28.7 (1.7)	30.1 (2.4)

Table 5. Average inflorescence length (cm) (±95% C.I.) of P. dilatata in relation to microhabitats of the St. Phillip's study site.

year	open mat	shrub zone	obscured areas
1990	7.3 (0.7)a n=21	8.3 (0.8)b n=36	10.1 (1.1)c n=17
1991	8.1 (0.7)a n=42	8.3 (0.6)a n=47	10.4 (1.2)b n=24
1992	8.0 (0.7)a n=31	8.8 (0.7)a n=41	9.8 (0.8)b n=22
Total	7.8 (0.4)	8.5 (0.4)	10.1 (0.6)

note: statistically similar averages ($p<0.05$, Tukey-Kramer method) have the same subscript within a given year.

Table 6. Mean plant heights (cm) (±95% C.I.) for P. dilatata in relation to microhabitats of the St. Phillip's study site.

year	open mat	shrub zone	obscured areas
1990	23.4 (2.2)a n=21	31.0 (2.3)b n=36	33.6 (3.1)b n=17
1991	28.5 (1.6)a n=42	29.3 (1.8)b n=47	31.9 (2.6)b n=24
1992	26.2 (1.7)a n=31	28.2 (1.4)b n=41	31.3 (2.3)b n=22
Total	32.0 (0.9)	39.8 (1.2)	41.2 (1.6)

note: statistically similar averages ($p<0.05$, Tukey-Kramer method) have the same subscript within a given year.

In 1990 each microhabitat had significantly different inflorescence lengths, but in 1991 and 1992, only plants from the obscured areas had inflorescences significantly longer than plants from the open areas or shrub zone.

The inflorescences from obscured areas were longer, but with similar numbers of flowers compared with the other microhabitats. This resulted in a looser arrangement of flowers on the spikes of those plants from obscured areas.

The mean plant height in all three years was significantly taller in the shrub zone and obscured areas than on the open mat (Table 6). Plants from the shrub zone and obscured areas were about 8 cm taller than those from the open mat.

The size of the various flower characters (Figure 2) measured fell within the values recorded for P. dilatata from continental North America populations (Table 7).

3.1.3 Breeding System

P. dilatata is self-compatible but not autogamous. When 10 plants (232 flowers) were covered with nylon mesh to exclude any potential pollinators, there was 0% capsule set. This indicates that an insect vector is required.

Table 7. Comparison of the size ranges (mm) among various flower characteristics of P. dilatata in Newfoundland and mainland North America.

Reference	dorsal sepal	lateral sepal	petal	lip	spur
Case 1964	3-7 X 3-4	4-9 X 1-2	4-9 X 2-4	5-10 X 2-6	5-10
Luer 1975	3-7 X 1.5-4	3-8 X 1-3.5	3-8 X 1.5-4	5-10 X 2-5	5-10
Boland 1993	4-6 X 2.5-4	5-8 X 2-3	5-7 X 2.5-4	6-8 X 3-4	6-8

Artificial outcrossing resulted in 100% capsule set (4 plants, 115 flowers), as did geitonogamy (4 plants, 97 flowers) and self-pollination (4 plants, 82 flowers). This indicated that all of the flowers on an inflorescence could potentially produce capsules (Table 8).

3.1.4 Pollinaria Removal

Pollinaria removal by pollinators was fairly consistent over the 10 day observation period. Only during wet weather was pollinaria removal noticeably depressed. At the end of the study period, 527 (70.6%; range = 47.2-76.8% per plant) of a total of 746 pollinaria had been removed from the 15 plants. With respect to the pollinaria removed, 15% were removed by day and 85% by night.

Of 373 flowers observed in the pollinaria removal study, 208 (55.8%; range = 46.8-71.4% per plant) of the stigmas had pollinia deposited on them. All pollinations resulted in the formation of seed capsules. With respect to pollinia deposition, 9.1% were deposited by day and 90.9% were deposited by night.

A strong positive correlation, r_c=0.955, was observed between polliniaria removal and the number of flowers per inflorescence.

Table 8. Overview of the results from the experimental pollinations of P. dilatata.

Treatment	# plants	Total # flowers	Total # fruit	% fruit set
bagged	10	232	0	0
geitonogamy	4	97	97	100
out-crossed	4	115	115	100
self-pollinated	4	82	82	100

3.1.5 Pollinator Observations

Observed insect activity was quite low over the three year period. Most observations did not occur until the population of orchids had reached their peak blooming. P. dilatata was visited mainly by lepidopteran insects (Table 9). Some dipteran and bumblebees, Bombus spp., were seen to visit the flowers, but remained on the flowers for less than 20 seconds. They did not effect pollination. The insects listed in Table 9 were mostly captured at the St. Phillip's site. The exceptions were Papilio brevicauda which were seen at the Cape Freels site and P. glaucus canadensis which was observed by B.S. Jackson (personal communication) in the Wooddale region.

Lepidopteran visitors were distributed among five families including two families of moths, Noctuidae and Notodontidae; two families of butterfly, Papilionidae and Nymphalidae; and skippers, Hesperiidae. All confirmed pollinators were in the Noctuidae or Hesperiidae families. Butterflies are fast fliers and although several were observed to probe the flowers for up to a minute, none were successfully captured to determine if they effected pollination.

Table 9. Pollinators and visitors of P. dilatata flowers (1990-1992).

Order and Family	*Species*	Status
Lepidoptera		
Papilionidae	Papilio brevicauda	uncertain
	P. glaucus canadensis	uncertain
Nymphalidae	Boloria selene terraenovae	uncertain
Hesperiidae	Thymelicus lineola	uncertain
	Polites coras	pollinator
Noctuidae	Autographa flagellum	pollinator
	A. pseudogamma	pollinator
	Phlogophora iris	pollinator
	Syngrapha rectangula	pollinator
	Pseudothyatira expultrix	pollinator
	Pseudaletia unipuncta	pollinator
	Aletia oxygala	pollinator
	Chrysaspidia putnami	visitor
	Rhyacia quadrangula	visitor
	Cerapteryx graminis	visitor
Notodontidae	Ichthyura apicalis	visitor
Hymenoptera		
Apidae	Bombus spp.	visitor
Diptera		
Calliphoridae		visitor
Syrphidae	3 unidentified species	visitor

Noctuid pollinators were observed mostly on calm, warm evenings. However, some moths may be active pollinators by day as attested by one active individual observed at 10:35 am. Peck's skipper, Polites coras, is strictly a diurnal pollinator, most active on warm calm days. These pollinators would normally land on the lower portion of the inflorescence, then move upwards. Only a few flowers per inflorescence were visited before the pollinator would move to another plant. The skippers mostly visited a neighbouring plant, while the moths moved about at random. Pollinators remained on an inflorescence for an average of 41.3 seconds (95% C.I.± 9.8 sec.; n=46). The pollinaria were attached to the proboscis. Pollinators were observed to carry 1-5 pollinaria.

Most pollinators remained on an individual inflorescence for a shorter time period than is required for the pollinaria to rotate to the forward position (about a minute). This action keeps self-pollination to a minimum and depresses potential geitonogamy. Cross-pollination appears to be the primary pollination mechanism of P. dilatata, although geitonogamy and self-pollination could also occur.

3.1.6 Capsule Set

The prevailing weather during the blooming season of a plant can have a marked affect on the activity of the insect

pollinators and, hence, the potential capsule set of that plant. Table 10 gives an overview of the weather during each of the flowering seasons for P. dilatata at the St. Phillip's site. The mean temperature varied from 14.7°C in 1991 to 18.9°C in 1990. Despite this, the overall capsule set was not significantly different among the three seasons. The mean percentage capsule set ranged from 47.7% - 56.0% (Table 2).

The distribution of the number of capsules was skewed to the right with the greater percentage of plants producing fewer than 20 capsules per plant (Figure 5). The distribution of percentage capsule set values was normally distributed for all three seasons with most plants having 41-60% of their flowers producing seed capsules (Figure 6).

Percentage capsule set in relation to inflorescence classes showed similar capsule set for all flower classes (Table 11). A significant positive correlation (r_{c1990}=0.583, p<0.01, n=74; r_{c1991}=0.689, p<0.01, n=113; r_{c1992}=0.635, p<0.01, n=94) existed between the number of flowers produced per inflorescence and the resulting number of capsules that developed. At this site, plant density had no effect on the percentage capsule set. Experimental population densities showed an individual plant per m^2 to have 52.7% capsule set while 20 plants per m^2 had 57.5% capsule set (Table 12).

Table 1?. Summary of daily temperatures (°C) during the 1990-1992 flowering seasons of P. dilatata growing in the St. Phillip's study site.

year	date	min.	mean low	mean	mean high	max.
1990	July 23-Sept. 6	4	14.1	18.9	23.4	31
1991	Aug. 1-Sept. 22	5	11.0	14.7	17.9	29
1992	July 25-Sept. 13	3	12.6	16.4	20.0	29

Figure 5. Frequency distribution of capsules per individual (1990-1992).

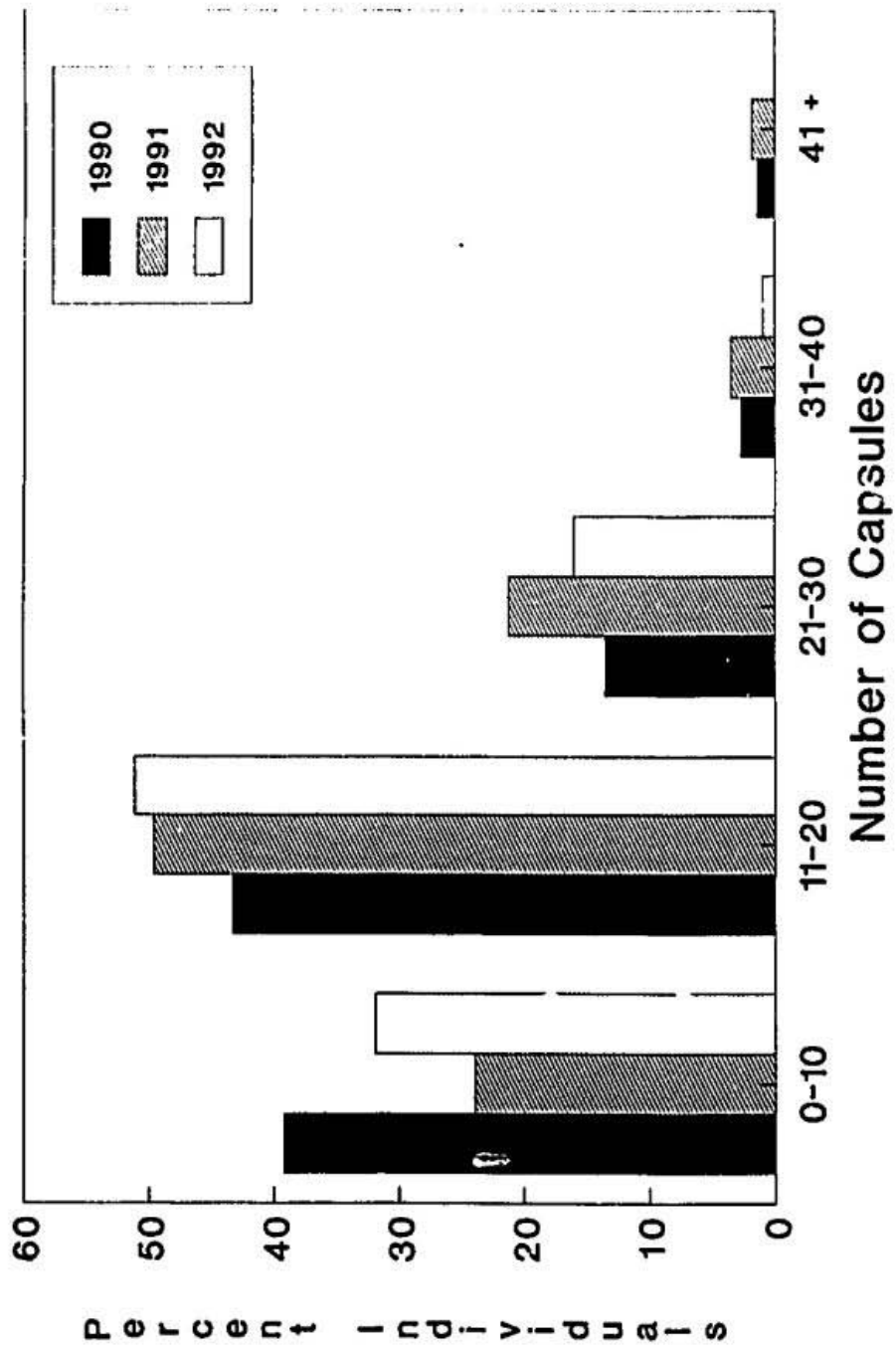

1990
1991
1992
Percent Individuals
0
10
20
30
40
50
60
0-10
11-20
21-30
31-40
41 +
Number of Capsules

Figure 6. Frequency distribution of percent capsule set among individuals (1990-1992).

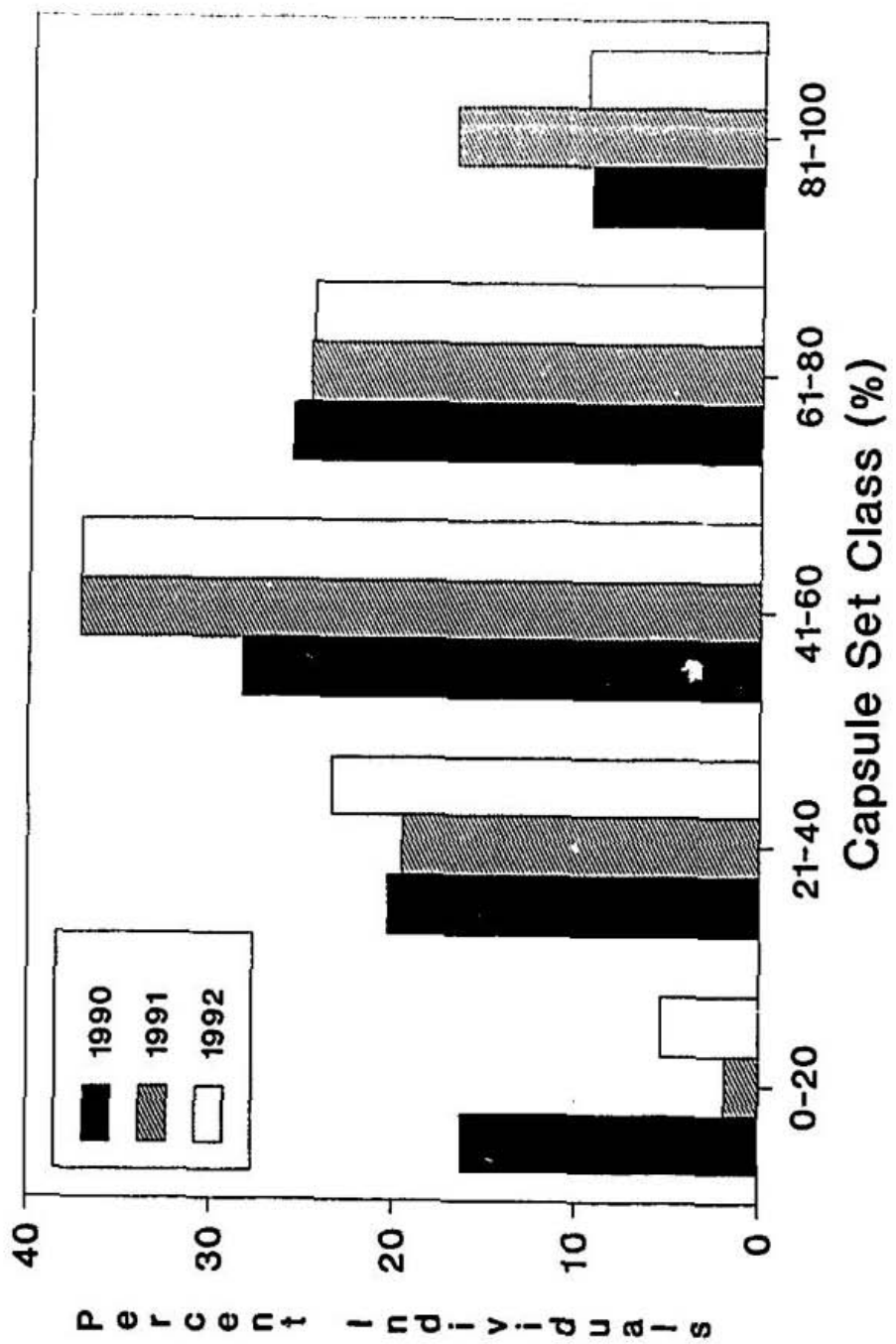

Percent Individuals
0
10
20
30
40
1990
1991
1992
0-20
21-40
41-60
61-80
81-100
Capsule Set Class (%)

Table 11. Average percentage capsule set (±95% C.I.) for P. dilatata plants from St. Phillip's pooled into three inflorescence classes.

inflorescence class	average % capsule set		
	1990	1991	1992
1-20	45.8 (15.8) n=14	61.0 (8.9) n=25	59.5 (10.1) n=20
21-35	47.3 (6.6) n=50	59.7 (5.3) n=50	50.2 (5.5) n=56
36 or more	53.9 (19.8) n=10	50.8 (5.8) n=38	51.2 (6.2) n=18

Table 12. Percentage capsule set in relation to experimental population densities of P. dilatata.

Number of plants per m^2	Number of flowers	Percentage capsule set (±95% C.I.)
1 (5 reps)	mean = 29.3	52.7 (22.1)
5	159	49.2 (21.2)
10	322	58.3 (14.6)
20	615	57.5 (9.6)

For the three year period, the total percentage capsule sets in the shrub zone and obscured areas were consistently greater than in the open mat, however, the differences were not significant (Table 13).

Pollinator activity was observed to decrease as the flowering season progressed. Changes in pollinator activity can be inferred by examining the percentage capsule set for the lower, middle and upper thirds of the inflorescence (Smith and Snow 1976, Cole and Firmage 1984). Percentage capsule set of the upper third was significantly lower than the middle and lower thirds for each microhabitat in all three years (Table 14).

3.1.7 Inflorescence Damage

The total number of plants present at the St. Phillip's site from year to year varied from 549 in 1990, 538 in 1991 to 489 in 1992. However, at the time of capsule harvest in mid- to late September, a major proportion of these plants had their inflorescences destroyed due to a combination of Lepidopteran larval-insect herbivory subsequently followed by fungal infection. In 1990, 86.5% of the flowers were destroyed; 79.0% in 1991 and 80.8% in 1992 (Table 15).

Table 13. Average percentage capsule set (±95% C.I.) for P. dilatata in relation to microhabitats of the St. Phillip's study site.

year	open mat	shrub zone	obscured areas
1990	42.8 (9.7) n=21	49.8 (8.9) n=36	50.5 (12.4) n=17
1991	52.0 (6.0) n=42	60.7 (5.8) n=47	58.4 (7.5) n=24
1992	48.4 (6.3) n=31	52.4 (7.3) n=41	56.2 (8.4) n=22
Total	47.7 (3.9)	54.3 (4.1)	55.0 (4.9)

Table 14. Average percentage capsule set (±95% C.I.) for three inflorescence regions of P. dilatata growing in St. Phillip's during the seasons of 1990-1992.

	Inflorescence Region			
Year	Lower Third	Middle Third	Upper Third	n
1990	64.7 (6.9)a	53.0 (7.4)a	26.5 (5.6)b	74
1991	64.5 (5.5)a	64.6 (5.0)a	38.4 (5.0)b	113
1992	66.7 (5.8)a	56.8 (4.8)a	34.2 (4.8)b	94
Total	65.3 (3.3)	58.1 (3.2)	33.0 (2.9)	281

note: statistically similar averages ($p<0.05$, T-method) have the same subscript within a given year.

Table 15. Percent of inflorescences destroyed by insect/fungal damage in each of the microhabitats at the St. Phillip's study site.

year	open mat	shrub zone	obscured areas
1990	95.0 (n=424)	62.1 (n=95)	43.3 (n=30)
1991	81.5 (n=417)	51.7 (n=91)	20.0 (n=30)
1992	91.9 (n=382)	47.4 (n=78)	24.1 (n=29)

Most of this damage was associated with the microhabitat of the plants. For all three seasons, the damage was most pronounced in populations of P. dilatata growing on the open mat (mean destroyed = 89.5%), with the least damage occurring in obscured areas (mean destroyed = 29.1%).

Damage was also significantly associated with the number of seed capsules produced per plant (Spearman rank correlation $r_{s(1991)} = 0.814$, $p<0.02$, $n=113$; $r_{s(1992)} = 0.731$, $p<0.025$, $n=94$).

The small entrance holes of the Lepidopteran larvae were observed along the hollow peduncle and the immature capsules. Browsing was evident along the inner surface of the stem and within the seed capsules. This initial insect damage was usually followed by a secondary fungal infection which would then cause the entire inflorescence to turn brown and collapse. Such damage resulted in very depressed seed production in each of the three years.

3.2 Results from Inter-site Study

The mean number of flowers per inflorescence was comparable among the three Newfoundland populations; 26.1 at Cape Freels, 26.4 at St. Phillip's and 27.1 at Butterpot Park. These means were also comparable to the mean flower production of a population growing in a subalpine fen along Cameron Lake,

Alberta (26.5) (Table 16).

Among the Newfoundland populations, the mean plant height was significantly shorter at Cape Freels (mean = 28.5 cm) than at Butterpot (mean = 33.8 cm) or St. Phillip's (mean = 32.2 cm). Plants from Cameron Lake were significantly taller (mean = 36.4 cm) than those at St. Phillip's and Cape Freels, but not at Butterpot ($p<0.05$, T-method; Table 16).

Mean inflorescence lengths among the four sites were comparable between Cape Freels and St. Phillip's. Mean inflorescence lengths were significantly greater at Cameron Lake and Butterpot ($p<0.05$, T-method; Table 16).

The mean percentage capsule set among the three Newfoundland populations did not differ significantly, although capsule set at Cape Freels was much higher than at the other two sites ($p=0.065$, ANOVA). Percentage capsule set at Cameron Lake (66.8%) was significantly higher than at St. Phillip's (50.2%) or Butterpot (46.8%), but not significantly higher than at Cape Freels (59.1%; Table 16).

Inter-site examination of percentage capsule set for each third of the inflorescence gave similar results to those obtained from the three year within-site study conducted at St. Phillip's. In all locations, the upper third had a significantly lower percentage capsule set than the middle

Table 16. Summary of results (±95% C.I.) obtained from populations of P. dilatata growing in open areas at four sites (n=30 plants for each site).

Location	mean # flowers per plant	average % capsule set per plant	mean inflorescence length per plant (cm)	mean plant height (cm)
St. Phillip's	26.4 (3.4)	50.2 (7.2)a	7.9 (0.7) ab	32.2 (1.7)b
Butterpot	27.1 (2.3)	46.8 (9.5)a	8.8 (0.8) b	33.8 (2.0)bc
Cape Freels	26.1 (3.8)	59.1 (6.6)ab	7.2 (0.6) a	28.5 (1.9)a
Cameron Lake, Alberta	26.5 (3.6)	66.8 (8.1)b	8.3 (0.8)b	36.4 (2.5)c

note: statistically similar averages ($p<0.05$, T-method) have the same subscript within a given treatment.

and/or lower third (Table 17). The percentage capsule set on the lower and middle thirds of the inflorescence was comparable among the four populations, but the percentage capsule set on the upper third of those plants from Cameron Lake was significantly higher than those obtained from the three Newfoundland populations.

Despite high inflorescence damage at the St. Phillip's site, no insect or fungal damage was observed in populations of P. dilatata growing at Cape Freels, Butterpot Park or Cameron Lake.

Table 17. Average percentage capsule set (±95% C.I.) for three inflorescence regions of P. dilatata growing in four locations (n=30 plants for each site).

	Inflorescence Region		
Location	Lower Third	Middle Third	Upper Third
St. Phillip's	61.7 (9.9)a	53.7 (8.1)a	29.8 (7.5)b
Butterpot	54.9 (12.0)a	52.3 (10.4)ab	34.0 (10.9)b
Cape Freels	79.3 (8.9)a	63.6 (9.8)a	34.3 (11.1)b
Cameron Lake	74.7 (10.0)a	74.3 (9.1)a	52.4 (10.3)b

note: statistically similar averages ($p<0.05$, T-method) have the same subscript within a given location.

4. Discussion

4.1 Phenology

The blooming season of P. dilatata in Newfoundland extends over a relatively long period of time; approximately 51 days (range = 43-59 days). Long blooming seasons have also been documented for populations of this orchid in Maine, where they bloom from 46-60 days (Heinrich 1976). Populations growing in subalpine fens of southwest Alberta also bloom for approximately two months (C. Boland, personal communication).

Long-lived flowers prolong the availability of flowers to the pollinator and are generally more typical of early blooming species than later blooming species such as P. dilatata. Primack (1985) classifies long-lived flowers as those which last for over 10 days. The flowers of P. dilatata can be classified as long-lived since mean flower longevity is about 17 days. An extended blooming period and sequentially produced long-lived flowers are an advantage to P. dilatata allowing it to capitalize on low pollinator visitation rates, especially during prolonged periods of poor weather.

During the 1990-1992 flowering seasons, the peak bloom of P. dilatata occurred from as early as August 7 in 1990 to as late as August 21 in 1991. These peaks are related to the

daily mean temperature which was highest in 1990 (18.9°C) and lowest in 1991 (14.7°C; Table 10).

Luer (1975) described the blooming season of P. dilatata to extend from May into August. P. dilatata, in Newfoundland, generally blooms from late June to mid-September, extending the previously-documented season by nearly a month. The blooming season in sub-alpine populations in southwestern Alberta is comparable to that in Newfoundland; from mid-July to early September (C. Boland, personal communication).

The mean number of flowers per inflorescence for the St. Phillip's population of P. dilatata was remarkably consistent over the three year study period, ranging from 27.6 to 30.6 flowers per inflorescence. Consistent average flower production over several seasons has been previously documented for P. blephariglottis (Cole and Firmage 1984). Populations from two other Newfoundland populations and a population in southwest Alberta had comparable mean flower production (Table 16). Case (1964) found most plants of P. dilatata near the Great Lakes to produce 12-80 flowers per inflorescence, but he gives no indication of the mean flower production. This study determined that Newfoundland and southwestern Alberta populations have similar flower production ranges; 6-62 in Newfoundland, 12-52 in southwestern Alberta.

Previous studies on orchids from the P. dilatata-P. hyperborea complex have concentrated on P. stricta (Patt et al. 1989). Populations of P. stricta in Washington State had an average of 30 flowers per plant, with a range of 12-65. Populations of P. hyperborea from western and northern Newfoundland also averaged 25-30 flowers with a range of 8-58 (personal observations). A wide range of flower production with an average of about 30 flowers per inflorescence appears to be typical of this Platanthera complex.

Microhabitats did not affect the mean number of flowers produced per plant. During the three seasons of study, mean flower production from the three microhabitats ranged from 25.2 to 31.2 flowers per inflorescence. Cole and Firmage (1984) did not find that microhabitats affect mean flower production in P. blephariglottis. Thus, plants of P. dilatata could potentially produce similar numbers of seed capsules regardless of the microhabitat they inhabit.

4.2 Morphological Comparisons

The overall mean plant height and mean inflorescence length did not differ in the St. Phillip's population over the three year period. However, microhabitats did show a significant difference in these characteristics. For all three seasons, plants from the shrub zone and obscured areas

were taller than those from the open mat. Part of this difference was due to significant differences in the lengths of the inflorescences among the three microhabitats in all three seasons (Table 5).

In 1990, the inflorescences increased significantly in length from the open mat to obscured areas. In 1991 and 1992, this trend was also evident, but only plants from the obscured areas had significantly longer floral spikes. These differences may be explained on the basis of light regimes. Plants in more shaded locations become etiolated.

The mean number of flowers per inflorescence was not different among the microhabitats. The average inflorescence area (length of inflorescence X width of inflorescence) was also similar among the microhabitats (obscured = 18.2 cm^2, shrub = 19.7 cm^2, open = 20.3 cm^2). Plants from obscured areas were taller with a looser arrangement of flowers while those from the open mat were of shorter stature with a denser, more contracted flower spike, but the overall "target size" was similar among the three microhabitats. These results are similar to those found by Cole and Firmage (1984). Their studies on P. blephariglottis showed plants to be taller in shaded areas but to produce a similar "target size" to plants growing in the open mat.

Comparisons among the four site locations showed significant differences in mean plant height and inflorescence length. These differences are assumed to be mostly due to different environmental factors at these sites. Plants from Cape Freels were very exposed, growing within reach of the ocean spray and plants there were significantly shorter in height and spike length than those from the other three sites. Plants from Cameron Lake, Alberta were the tallest of the four sites. These plants were the most sheltered of the four sites, being surrounded by 20-30 m conifers which may have effectively reduced wind speed.

Floral measurements were similar between Newfoundland populations and those documented for mainland populations (Table 7). Plant taxonomists usually rely on floral characteristics to classify a species since these characteristics are not influenced by the environment as much as leaf morphology or plant height.

Documented heights for P. dilatata in Newfoundland and subalpine areas of southwestern Alberta were at the lower end of those previously documented for this orchid. Case (1964) gives the height range for P. dilatata as 10-100 cm. Luer (1975) states they may grow 100 cm+, Petrie (1981) up to 125 cm. Luer (1975) also indicates that plants generally produce about 12 leaves. Populations of P. dilatata from Newfoundland

and southwestern Alberta produced 4-8 leaves and averaged less than 40 cm in height.

Shorter plants have been documented for other Newfoundland orchids. Populations of P. lacera (Michx.) Don. var. terrae-novae (Fern.) Luer on the island are known to have fewer leaves per plant than populations of this orchid on the mainland (Luer 1975). Previous studies on other Newfoundland orchids; Arethusa bulbosa L., Calopogon tuberosus (L.) BSP and Pogonia ophioglossoides (L.) Ker., showed their floral characteristics to be similar to those of mainland plants (Boland 1989).

4.3 Breeding System

The flowers of P. dilatata are self-compatible but not autogamous. Exclusion of possible insect pollinators prevented any seed capsule production, indicating that an insect vector is required. When 97 flowers were pollinated geitonomously, all resulted in the formation of a seed capsule, demonstrating that flowers are receptive to pollinia from the same inflorescence. Flowers which were self-pollinated also resulted in 100% capsule set, indicating self-compatibility (Table 8).

Self-compatibility has been noted for many orchid species

but pollination mechanisms mostly favour outcrossing (Van der Pijl and Dodson 1966, Smith and Snow 1976, Cole and Firmage 1984). Rotation of the caudicles so that the pollinaria are in a forward position for deposition on the stigma takes about a minute. As a result, self-pollination could be assumed to be a rare incident, however, some insects probed an inflorescence for over a minute and could have effected geitonomous pollination.

It should be noted that the percentage of viable embryos were not compared between the outcrossed and self-pollinated plants. Some orchids will produce normal capsules upon selfing but functional seeds are reduced (W.R. Stoutamire, personal communication). This feature suggests that pollination mechanisms favour outcrossing.

The flowers of an inflorescence of P. dilatata open sequentially from bottom to top, thus the bottom flowers would presumably be the first to be pollinated and produce capsules. If resource limitation exists it would prevent resources from being allocated to any developing capsules on the upper portion of the spike. Even if capsule production is scattered over an entire inflorescence, the upper capsules could be aborted as a way of saving the energy which would be required to enlarge a large section of the peduncle. However, artificially-pollinated inflorescences with 100% capsule set

did not abort any seed capsules. Naturally-pollinated plants with 100% capsule set also matured all of their capsules. This suggests that seed capsule production may not be resource limited. In addition, if resources were limited, percent seed capsule production would be expected to decrease with increased flower production. However, in this study, flower production was positively correlated with seed capsule production ($r=0.811$).

Artificial pollination resulted in much higher fruit set than natural pollination, indicating that this orchid may be pollinator-limited. Previous studies on other non-autogamous species of Platanthera have also shown them to be pollinator-limited (Smith and Snow 1976, Cole and Firmage 1984, Patt et al. 1989, Robertson and Wyatt 1990).

Evidence for pollinator-limited systems are not confined to the Orchidaceae. Schemske et al. (1978) found that hand-pollinated plants of Erythronium albidum Nutt. (Liliaceae) had 78% of their flowers set seed compared to 33% when naturally pollinated. Willson et al. (1979) showed 82.3% of hand-pollinated Phlox divaricata L. (Polemoniaceae) blossoms to produce seed compared to 58% when naturally pollinated.

However, Janzen et al. (1980) warns against interpreting seed production from one year's seed or fruit production as

proof of pollinator limitations. Only if hand-pollination consistently produces higher fruit set over an extended number of years can the idea of resource limitation be dismissed. In the long tern, plants which produce a high fruit set in one year, may fail to reproduce in a subsequent year. Such evidence has been documented by Primack and Hall (1990) for Cypripedium acaule and Ackerman (1989) for Encyclia krugii.

Individual plants of P. dilatata were not followed from year to year, but it may be assumed that high fruit set in one year could lead to lower growth rates and/or flower production in a subsequent year. For P. dilatata, lifetime reproductive output may be a balance between pollinator and resource limitations.

4.4 Pollinaria Removal

Pollinaria removal is a direct reflection of pollinator activity. The population of P. dilatata in St. Phillip's had an average of 68.2% of pollinaria removed (range = 47.2-76.8% per plant).

Similar rates of pollinaria removal have been documented for other Platanthera species. Patt et al. (1989) found pollinaria removal rates of 57-78% for populations of the closely related P. stricta; Robertson and Wyatt (1990) found

removal rates of 64-84% for populations of P. ciliaris (L.) Lindl. This suggests that, for P. dilatata and these other documented Platanthera species, there are fairly high levels of pollinator visitations compared with the normally low pollinator visitation rates for orchids in general (Schemske 1980, Acherman and Montero 1985, Calvo 1990).

No previous studies have investigated pollinaria removal to determine if it occurs by night or by day. This study confirmed that most pollinaria removal and, hence, pollinator activity occurred at night. However, limited pollinaria removal was found to occur by day indicating P. dilatata has both nocturnal and diurnal pollinators.

There was a significant positive correlation ($r_s = 0.955$) between pollinaria removal and the number of flowers per inflorescence. This indicates that the number of pollinaria removed generally increases with inflorescence size. Willson and Rathcke (1974) found the number of pollinia removed to increase with inflorescence size in Asclepias. This suggests more insect visits to larger inflorescences.

The entire pollinarium is rarely deposited onto the stigma. Deposition is mostly in the form of several massulae. Duckett (1983) found that pollination of P. lacera by several massulae was as effective in producing a seed capsule as the

deposition of the entire pollinaria. Gregg (1991) found that neither capsule set nor maturation of the capsules was affected by the number of pollen grains deposited on the stigmatic surface of Cleistes divaricata (L.) Ames. However, she found that the number of pollen grains deposited will affect the number of seeds produced per capsule. Determination of the seed production per capsule as a function of the number of pollen massulae deposited was not done for this study. Unmanipulated plants had a capsule set rate of 47-55% and presumably would have similar percentages of total flowers with pollen massulae deposited on the stigma. Pollinaria removal and massulae deposition both indicate regular pollinator visitations during the blooming season.

4.5 Pollinators

P. dilatata, like several other members of the genus, is pollinated by Lepidopteran insects. Although this orchid has a relatively high percentage capsule set, observed pollinator activity was quite low over the three year study. The major pollinator was night-flying noctuid moths (Table 9) which were most active during the two hours from dusk to dark. The activity of the moths was determined by the prevailing weather, temperature in particular. No moth activity was observed during rainy or windy weather, but foggy calm weather did not deter activity. Most activity was seen on relatively

calm, clear evenings. Other studies on orchids pollinated by night-flying moths indicated that moth activity ceased when night temperatures dropped below 15°C (Smith and Snow 1976, Cole and Firmage 1984). However, I observed moths actively probing flowers when the air temperature was as low as 12°C.

All documented noctuid species, except Phlogophora iris, are distributed across Canada, Alaska and the northern United States, essentially coinciding with the distribution of P. dilatata. P. iris is found only in eastern North America (Morris 1980). Noctuid moths have been previously documented as pollinators of other Platanthera species (Stoutamire 1971, Catling 1985) and at least one species, Aletia oxygala, has been documented previously as a pollinator of the closely-related P. huronensis (Catling and Catling 1989). The other species of noctuid moths seen visiting could potentially be pollinators as well but, without the attachment of pollinaria, their status has to remain as uncertain for the present. It may be assumed that many other species of noctuid moths could also be potential pollinators of P. dilatata.

Moths are primarily attracted to P. dilatata due to the odour produced by the flowers. Moths can follow the odour trail of a single plant as well as a group of plants (Williams 1983). This was reflected in the plant density experiments which showed that plants produce comparable levels of capsule

set whether they ocurred as isolated plants or if there were 20 plants per m^2.

Microhabitats had no effect on seed capsule production. Olfactory cues can allow moths to find plants which are obscured under trees and shrubs. Smith and Snow (1976) and Cole and Firmage (1984), who studied the moth-pollinated P. blephariglottis, also found microhabitats to have little effect on fruit set.

Several diurnal Lepidopteran species were observed to infrequently probe the flowers of P. dilatata. Peck's Skipper, Polites coras, was the only diurnal Lepidopteran verified as a pollinator. This skipper is widespread throughout eastern North America and has been frequently seen to visit a wide range of summer flowers (Morris 1980).

The European skipper, Thymelicus lineola, was first seen in Newfoundland in 1976 (Jackson 1978). Since that time, it has steadily increased in numbers. Only a few individuals were seen collecting nectar in the St. Phillip's site but none were observed to carry pollinaria. Since this skipper is introduced, it would not have been a regular pollinator of this orchid.

Papilio brevicauda was only observed to visit P. dilatata at the Cape Freels site. The short-tailed swallowtail is usually found near the coast. Its distribution is determined by that of its host plant, Ligusticum scothicum L., which is coastal in its distribution. B.S. Jackson (personal communication) observed Papilio glauca canadensis actively probing flowers of P. dilatata in the Wooddale region of western Newfoundland.

Day-flying Lepidopteran pollinators use colour as their primary attractant (Van der Pijl and Dodson 1966). Butterflies and skippers are generally attracted to yellow, orange or red flowers. However, Schemske et al. (1978) noted that many white-coloured spring flowers are attractive to pollinators since they contrast sharply with the brown and green of the surrounding vegetation. A similar situation may exist in this fen where the white flowers of this orchid contrast with the greens and browns of sphagnum moss, sedges and grasses. In addition, the flowers of this orchid sparkle due to light reflection and refraction, further enhancing the visual attraction of the orchid.

Diurnal odour production in orchids is generally associated with butterfly pollination (Van der Pijl and Dodson 1966). P. dilatata has a northern distribution and may be exposed to extended periods of cool night temperatures when

moth activity could be depressed. Maintaining odour production during the day may have the advantage of attracting day-flying lepidopteran pollinators to this orchid. This can further aid in the plant's fitness by allowing at least some pollination when night conditions are unfavourable for nocturnal moth activity.

Bumblebees (Bombus spp.) were not observed to be pollinators of P. dilatata. Studies on the closely-related P. stricta and P. huronensis found Bombus to be active pollinators of these orchids (Patt et al. 1989, Catling and Catling 1989). Bumblebees were quite common in the study areas but, during the blooming season of this orchid, the bees concentrated their foraging efforts on Solidago uliginosa and Aster nemoralis. The St. Phillip's site had several co-blooming plants of the orchid Spiranthes romanzoffiana Cham. These were actively probed by bees while nearby plants of P. dilatata were ignored. Presumably, the proboscis of Bombus is not long enough to successfully forage for nectar from this orchid.

Both the within-site and between-site studies showed that pollinator activity decreased over the blooming period. In all populations, the upper third of the inflorescence had a significantly lower percentage capsule set than the bottom and middle thirds. There are several possible reasons for the

apparent drop in pollinator activity. Being later in the season, the daily temperatures, especially the night temperatures, were much lower than earlier in the season (personal observation). Since the pollinators are directly affected by temperature, the pollinator activity would naturally decrease later in the season. Direct observation of pollinators showed this drop in activity.

Morris (1980) noted that many noctuid moths, including most of the verified moth pollinators, cease to be in flight after late August. Due to life history strategies, populations of pollinators may naturally decrease later in the flowering season of the orchid. A lowering of the pollinator population will subsequently lower potential rates of pollination.

There is another possible factor contributing to lower capsule set on the upper third; many of the upper flowers on a spike never fully opened. In these flowers, the labellum was "caught-up" in the rim of the hood (Figure 2). Although such flowers were still accessible to visitors, approaches were restricted to the sides rather than from the front. Pollinaria could still be removed but due to the obstructing labellum, pollinators were rarely in the correct position to deposit pollinia onto the stigma. P. hyperborea (personal observation) and P. huronensis (Catling and Catling 1989) also

show this phenomenon.

4.6 Prevention of Cross-pollination

The uncommon P. orbiculata (Pursh) Lindl. is the only other species of Newfoundland Platanthera, which has been documented as being pollinated by noctuid moths (Catling 1985). The blooming season of this species may overlap with that of P. dilatata but the former species usually grows in damp coniferous forest (personal observation), a habitat not favoured by P. dilatata. In addition, the pollinaria of P. orbiculata is deposited onto the eyes of the moth, rather than the proboscis. If a moth should be carrying pollinaria from P. orbiculata when it visits a bloom of P. dilatata, the pollinaria would not be in the correct position to effect cross-pollination. The combination of habitat differences and pollinaria deposition sites effectively prevents hybridization between these two species.

The skipper, Polites coras, is also a documented pollinator of P. blephariglottis in Maine (Cole and Firmage 1984). Although P. blephariglottis was absent from the study sites, this orchid often grows sympatrically and co-blooms with P. dilatata (personal observations). Assuming that P. coras is also a pollinator of P. blephariglottis in Newfoundland, it is possible for this skipper to visit both

orchids and contain pollinaria of both. However, pollinaria from P. blephariglottis are deposited on the eyes of P. coran (Cole and Firmage 1984) while pollinaria from P. dilatata are deposited on the proboscis. Hence, neither pollinaria would be in the correct position to effect cross-pollination of these two orchid species.

4.7 Capsule Set

Orchids are generally characterized by low capsule set (Darwin 1877, Thien and Utech 1970). Those that lure pollinators by deception (i.e., offer no food reward) often have a percentage capsule set less than 10% (Mosquin 1970, Thien and Marcks 1974, Ackerman 1975, Ackerman 1981, Boland and Scott 1991), while some orchids which provide food rewards have been found to have a percentage capsule set over 50% (Nilsson 1978, Ackerman and Mesler 1979, Cole and Firmage 1984, Patt et al. 1989, Robertson and Wyatt 1990). Observed percentage capsule set of P. dilatata ranged from 46.8-66.8% and was comparable to levels observed in other orchids offering rewards.

Overall percentage capsule set within the St. Phillip's site was remarkedly consistent over the three flowering seasons. When Cole and Firmage (1984) followed a population of P. blephariglottis over a three year period, they found the

percentage capsule set to be similar in two years but dramatically lower in a third season. In their study, the season of lower capsule set had nearly twice the number of flowering plants than during the other two seasons. They suggested that low pollinator-to-plant ratio in that season may have resulted in the lower percentage capsule set. In the St. Phillip's site, the number of blooming plants varied little (489-549) thus, if the population of pollinators also varied little, the pollinator-to-plant ratio would be relatively consistent. This may explain the similar percentage capsule set noted for the three seasons.

The overall percentage capsule set in St. Phillip's (50.2%), Butterpot (46.8%) and Cape Freels (59.1%) was comparable, indicating that these eastern Newfoundland populations have consistent pollinator activity. Cameron Lake, Alberta, had significantly higher percent capsule set (66.8%) than St. Phillip's and Butterpot, but not higher than Cape Freels. Although there is no direct evidence, the higher capsule set in Alberta may suggest a higher population of pollinators and/or more favourable weather for pollinator activity during the blooming season of the orchid.

Several orchid studies have found the distribution of the number of capsules produced in a population to be skewed to the right, with most individuals producing few capsules and

few individuals producing many capsules (Janzen et al. 1980, Zimmerman and Aide 1989, Calvo 1990a, Calvo 1990b). My study also showed the distribution of the number of capsules to be highly skewed to the right. In all three years, over 70% of the individuals produced fewer than 20 capsules (Figure 5). This contrasts with the finding that over 80% of the individuals produce more than 21 flowers per inflorescence (Figure 3). Such a distribution is indicative of pollinator limitation.

The relationship between inflorescence size and resulting capsule set is very contradictive in orchids. Ionopsis utricularioides (Sw.) Lindl. (Montalvo and Ackerman 1987) and Epidendrum exasperatum (Calvo 1990) have decreasing percentage capsule set with increasing inflorescence size; Brassavola nodosa (L.) Lindl. (Schemske 1980) has increasing percentage capsule set with increasing inflorescence size; Calopogon tuberosus (Firmage and Cole 1988), Aspasia principissa Reichb.f. (Zimmerman and Aide 1989), Oeceoclades maculata (Lindl.) Lindl. (Calvo 1990b) and Platanthera blephariglottis (Cole and Firmage 1984) have no noticeable relationship between inflorescence size and resulting capsule set. Results from my study agree with those of the latter authors; there is neither an increase nor a decrease in the percentage capsule set with an increasing inflorescence size. Both small and large inflorescences had similar percentage capsule set (Table

11). Authors who found no relationship between inflorescence size and capsule set suggest that plants with larger inflorescences have a greater probability of setting at least one capsule. This could not be substantiated in my study since all plants, regardless of inflorescence size, set at least one fruit.

In the short term, inflorescence sizes of P. dilatata larger than the mean may have the selective advantage of greater seed production. In a year of favourable pollinator activity, these larger spikes would be visited more and thus would set a greater absolute number of capsules. Being a sequential bloomer, large spikes would lengthen the flowering season of that individual, increasing fitness by improving chances of setting fruit. Several recent orchid studies have shown that high fruit set may lead to a reduction in the future growth and/or reproductive levels of an individual orchid plant (Ackerman 1989, Snow and Whigham 1989, Primack and Hall 1990, Ackerman and Montalvo 1990). Thus, while capsule set for a particular year may be pollinator-limited, lifetime reproductive output of an orchid may be resource-limited. Although individuals plants were not followed, it may be assumed that, like other orchids, high capsule set one year may reduce future growth and/or reproductive levels in subsequent years. It appears that for P. dilatata, the mean flower production and hence lifetime reproductive success is

a reflection of evolutionary compromise; a balance between resource allocation and pollinator limitation.

4.8 Inflorescence Damage

Despite a relatively high percentage capsule set, the population of P. dilatata at St. Phillip's had few capsules survive to dehiscence as a result of lepidopteran larvae damage and fungal infection. In 1990, 86.5% of the individual inflorescences from the site were destroyed. It was first thought that this phenomenon was an isolated feature of that growing season, however, this high level of damage appears to be a regular feature of this site as 79.0% were destroyed in 1991 and 80.8% in 1992.

The lepidopteran larvae fed on the inner wall surface of the upper portions of the hollow stem, the inner sides of the capsules and the embryos. Neither the leaves nor the main plant stem showed evidence of being eaten. Such insect damage was evident as early as mid-August, however, the damage did not appear to be sufficient to cause the death of the entire inflorescence. In early to mid-September, secondary fungal infections caused the entire upper portion of the plant to wither and die.

It is assumed that the adult insects chose the

inflorescences of this orchid based on site. It is not known when the eggs are oviposited. By mid-September, most larvae had left the plants and the few remaining larvae were relatively large. It is not known if the larvae left to find new food sources or to pupate.

Insect damage and subsequent fungal infection were clearly affected by the microhabitat (Table 15). Most ravaged inflorescences were those from plants on the open mat, with 81.5-95.0% destroyed during the three year period. The percentage of destroyed inflorescences dropped to 47.4-62.1% for plants from the shrub zone and down to 20.0-43.3% in obscured areas.

There was a significant positive correlation between insect damage and the number of capsules per inflorescence. Inflorescences with high capsule set invariably had more damage than those with low capsule set.

Such high levels of insect/fungal damage to orchid inflorescences have not been previously mentioned in other reproductive biology studies of orchids. The highest level of destruction previously documented was 9.3% for a population of Cleistes divaricata (L.) Ames. growing in West Virginia (Gregg 1989).

Three consecutive years of high inflorescence mortality would suggest that this site may have been attacked by insect larvae for many years. While seed set is definitely depressed, populations of P. dilatata have not decreased substantially in the last three years. Either the plants are long-lived and, in the future, will slowly decrease in numbers or seed production by the remaining undamaged plants is sufficient to maintain this population of orchid.

This damage appears to be localized in the St. Phillip's site. Populations from Butterpot Park and Cape Freels showed no insect or fungal damage. However, these sites contained populations of less than 50 orchids, compared to about 500 in St. Phillip's. Cameron Lake, Alberta, with its small population of plants, also showed no signs of damage. Presumably, these populations may have been too small to be an effective food source for the larvae or the species of predatory insect was absent from those sites.

4.9 Future Studies

Since many orchids are quickly becoming endangered worldwide, any studies on this highly-evolved group will be of benefit, especially studies on short- versus long-term reproduction and the discrete relationships between orchids and their pollinators.

It would be interesting to repeat this study in western Newfoundland to determine if the findings only reflect the reproductive biology of P. dilatata in eastern Newfoundland populations or if the findings represent the entire population of P. dilatata on the island. Similar studies elsewhere in the distributional range of this orchid would also supply good comparisons. I hypothesized that odour production by day is an advantage to attract diurnal pollinators during periods of cool nights when noctuid moths are not active. Extensions of this study to the extreme northern distributional range of this orchid may give further insight. Presumably, night temperatures in such areas would be too cool for much noctuid moth activity. These moths may be active by day or diurnal Lepidoptera may be the primary pollinator.

The noctuid pollinators identified at the St. Phillip's site may represent only a small number of the potential noctuid moth species in Newfoundland which could pollinate this orchid. Similar studies done elsewhere would increase the list of known pollinators. Such studies may reveal other lepidopteran families as effective pollinators. Studies on the closely related P. stricta showed them to be pollinated by members of the Coleoptera, Trichoptera, Diptera and Hymenoptera as well as Lepidoptera (Patt et al. 1989). Studies on P. dilatata elsewhere may also show non-lepidopteran insects to be effective pollinators.

Several recent orchid reproductive biology studies describe capsule set as being pollinator-limited in the short-term while the lifetime reproductive output is resource-limited. To determine if this condition exists in P. dilatata, individual plants could be followed for several years to ascertain if high percentage capsule set in one season results in a negative effect on future growth. This situation does exist in other North American terrestrial orchids such as Tipularia discolor (Pursh) Nutt. (Snow and Whigham 1989) and Cypripedium acaule Ait. (Primack and Hall 1990).

This current study provides insight into the reproductive biology of P. dilatata which, until now, was virtually unstudied. This is the first detailed, long-term study done on a Newfoundland population of orchid and may serve as the basis for future studies on this advanced group of plants from the island.

5. Conclusion

In eastern Newfoundland, populations of P. dilatata bloom during a six week period from late July to early September, although this period may vary by two weeks depending on the mean summer temperature. About 30 long-lived flowers per spike are sequentially produced. While this orchid is self-compatible, an insect vector is required for successful capsule set. Pollinators were observed infrequently during the three flowering seasons. The primary pollinators are night-flying Noctuid moths which are most active during the two hours from dusk to dark. Limited pollination is also achieved by diurnal Hesperiidae.

Observed capsule set from the St. Phillip's populations of P. dilatata was remarkedly consistent over the three year period (47.7-56.0%). This indicates that pollinator activity was fairly constant during the blooming seasons of 1990-1992. These values were similar to those obtained from the other eastern Newfoundland sites.

Percentage capsule set was not affected by the microhabitat. This is mostly because this orchid uses scent as its primary attractant. Pollinators can detect the odour of this orchid whether plants are in the open or obscured under trees and shrubs. In addition, there is neither an

increase nor a decrease in percentage capsule set with an increasing inflorescence size.

Seed production was discovered to be very depressed in the St. Phillip's population due to lepidopteran larvae herbivory followed by secondary fungal infection. Such a high level of inflorescence damage may only be a local problem since the two other Newfoundland sites showed none of this damage.

Comparison between the Newfoundland populations and a population in southwestern Alberta did not indicate many differences. Percentage capsule set was significantly higher in Alberta than two of the three Newfoundland sites, but this may simply be due to a larger population of pollinators and/or more favourable weather for pollinator activity during the blooming season of the orchid.

All three Newfoundland populations as well as the Alberta population showed a significant drop in the percentage capsule set on the upper third of the inflorescence compared to the lower two thirds. There was no evidence of capsule abortion due to resource limitations, thus it may be concluded that the drop in capsule set was due to lower pollinator activity later in the season. This drop in activity may be the result of

cooler weather or a reduction in the population of pollinators.

P. dilatata is known to share its pollinators with other Platanthera species, notably, P. blephariglottis and P. orbiculata. However, placement site of the pollinaria on the insect, blooming season and/or habitat act to prevent hybridization among these species.

P. dilatata has a number of adaptations which allows for successful reproduction. An extended blooming season, sequentially-produced, long-lived flowers, long receptivity-time for flowers and continual odour production help maintain fairly high levels of capsule set, even during periods of unfavourable weather and low pollinator activity.

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